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SILVICAL *Characteristics* OF QUAKING ASPEN

(*Populus tremuloides*)

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THE SILVICAL REPORTS

During 1907 and the following several years the U. S. Forest Service issued a series of silvical leaflets which covered the broad characteristics of a considerable number of major timber species. Since then much new knowledge has accumulated--some of it published in a variety of sources. There is also a considerable store of unpublished silvical information in the files of the forest experiment stations, the forest schools, and some other agencies. To compile this information systematically and make it available to foresters generally, the Lake States Forest Experiment Station is preparing reports on 15 individual species. Similar reports are being prepared by the other Federal forest experiment stations. When completed, these individual species reports will provide the basis for a comprehensive manual of silvics for the important trees of the United States, to be published by the U. S. Forest Service.

This report is one of the series being prepared by the Lake States Station. A preliminary draft was reviewed by several members of our own Station staff and by a number of well qualified staff members of other forest experiment stations, colleges, and universities; Federal, State, and Provincial forestry organizations; and forest industry. Their comments helped the author to make this report more complete, more accurate, and more up to date. Especially helpful reviews were submitted by Professor Samuel A. Graham, School of Natural Resources, University of Michigan; Professor Scott S. Pauley, School of Forestry, University of Minnesota; E. J. Schreiner, Northeastern Forest Experiment Station; Leo Isaac, Pacific Northwest Forest and Range Experiment Station; and Edward M. Gaines and Lake S. Gill, Rocky Mountain Forest and Range Experiment Station.

Every effort has been made to ensure the accuracy and completeness of the information concerning the silvical characteristics of each species consistent with a brief treatment of the subject. We shall appreciate it, however, if any errors or omissions of important information are brought to our attention.

M. B. Dickerman

M. B. Dickerman, Director

Cover picture: A typical quaking aspen tree in Minnesota.
Drawing represents leaves.

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SILVICAL CHARACTERISTICS OF QUAKING ASPEN

(*Populus tremuloides* Michx.)

By

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Quaking aspen is the most widely distributed tree species in North America (66, 78);[2] it has a transcontinental range which covers more than 110 degrees of longitude and 40 degrees of latitude. Other common names include quaking asp, aspen, golden aspen, mountain aspen, trembling aspen, Vancouver aspen, poplar, trembling poplar, and popple (44). The terms "quaking" and "trembling" come from the fact that the leaves tremble in the slightest breeze because the leaf petiole is flattened at right angles to the leaf blade. The term "golden" refers to the brilliant gold and yellow of the foliage in the autumn.

DISTRIBUTION

The botanical range of the species (fig. 1) extends from Newfoundland and Labrador west across Canada along the northern limit of trees to northwestern Alaska; the southern boundary extends from New Jersey westward to Iowa and then northwestward to British Columbia; thence it extends south in high mountains of the western United States to southern California, Arizona, New Mexico, and Trans-Pecos Texas. Numerous outliers occur south of the main range (44).

The commercial range of aspen[3] (fig. 1) is confined chiefly to the Lake States and parts of New England, Manitoba, Saskatchewan, and Alberta. However, many stands in the Rocky Mountains and southwestern United States are also of excellent quality and occur in commercial volumes. The species is also quite abundant in the Ottawa Valley, Nippissing and eastern Algoma, the middle St. John Valley, and parts of the northern clay belt of eastern Canada (29).

1/ Maintained by the Forest Service, U. S. Department of Agriculture, at St. Paul 1, Minn., in cooperation with the University of Minnesota.

2/ Underlined numbers in parentheses refer to literature cited, page 23.

3/ Commercial range is defined as that portion of the botanical range within which the species grows to commercial size and is a major or important species in the type.

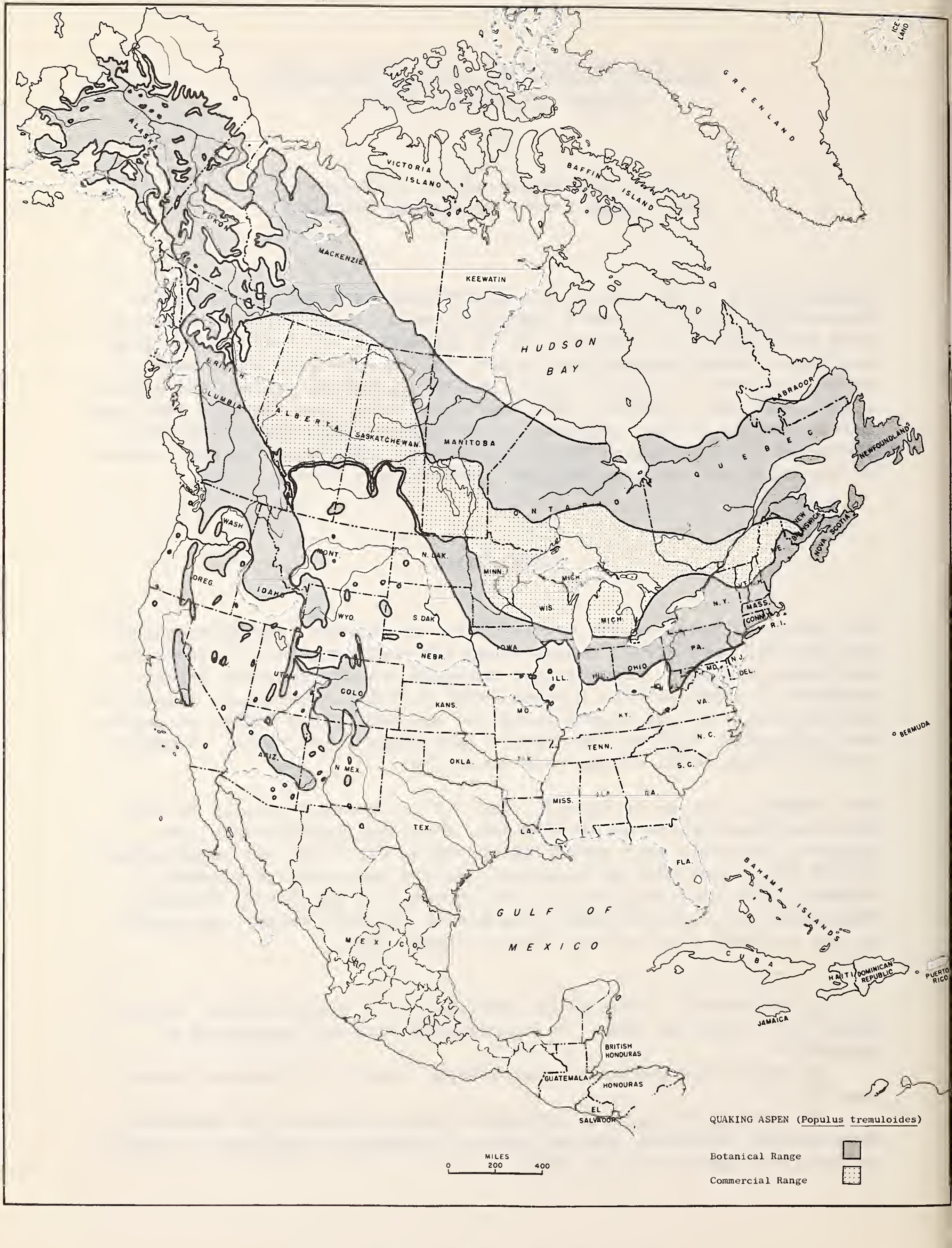

Figure 1.--Botanical and commercial range of quaking aspen

HABITAT CONDITIONS

As indicated by its tremendous geographic range, quaking aspen is an extremely adaptable species. It grows under a wide variety of climatic and edaphic conditions. In general it may be characterized as being a cold-tolerant and moisture-needing species.

Climatic Factors

Climatic conditions vary greatly over the range of the species, especially with respect to winter minimum temperatures and the amount of precipitation received.

In the interior of Alaska near the northern limit of aspen, temperatures as low as -78° F. have been recorded with January temperatures averaging about -22°. Summer temperatures have exceeded 100°, although the July average is about 61°. Precipitation is relatively light, amounting to only about 7 inches annually with slightly more than 3 inches falling during June, July, and August (37). The growing season averages about 81 days (45). In Alaska and northwest Canada, a portion of the aspen range lies within the permafrost zone.

At the eastern end of its range, in the Maritime provinces of Canada, the climate is considerably milder and more humid. In the vicinity of Gander, Newfoundland, winter low temperatures of about -30° F. have been recorded, although the average January temperature is about 20°. Maximum summer temperatures of about 90° have been recorded, although the July average is about 60°. Precipitation is relatively heavy, averaging about 40 inches annually, 10 inches of which falls during June, July, and August. Snowfall is extremely heavy in this area and amounts to 120 inches or more per year (80).

Fort Wayne, Ind., typifies some of the warmer portions of the aspen range. The coldest recorded temperature here is -24° F., but January averages about 27°. The warmest temperature recorded is 106°, although the average July temperature is 74°. Annual precipitation averages about 34 inches, with about 13 inches falling during the period of May through August. The average duration of the frost-free period is about 176 days (36).

In the central Rocky Mountains, where altitude plays an important role in the distribution of the species, the lower limit of its occurrence coincides roughly with a mean annual temperature of 45° F. (8). This isotherm also coincides approximately with the lower limit of aspen in

Arizona.[4] In Canada the average July isotherm of 55° coincides roughly with the northern limit of the species (29).

Aspen generally requires a moderate amount of precipitation, although it can withstand dry climatic conditions if its roots can reach a supply of moisture (85). The species is quite frost-hardy, but young sprouts which emerge late in the growing season are sometimes killed back by early autumn frosts because they failed to "harden off" soon enough. Also, late spring frosts in depressions may kill the new foliage within a certain zone.

Edaphic Factors

Quaking aspen grows on a great variety of soils ranging from shallow rocky soils and loamy sands to heavy clays. In the Lake States it is found on all kinds of soils. Only occasional scattered trees, however, occur on the coarser sands of glacial outwash, the shallowest soils of the rock outcrops, and in some sphagnum bogs, and they seldom attain commercial size (39). In Minnesota, following the catastrophic drainage of two lakes, the species was able to establish itself successfully on drained sedimentary peat (50), and in central Wisconsin it has seeded in on the ashes of burned-out peat following drainage.[5] In the West it has even become established on volcanic cinder cones (21).

Growth and development, however, are strongly influenced by soil conditions (8, 60, 90). Some of the best stands of quaking aspen occur in the northern portions of the Lake States and in Manitoba and Saskatchewan on soils which have developed from a gray glacial drift rich in lime (74). In addition to having an abundance of lime, the best aspen soils are usually porous, loamy, and humic (89).

Growth on sandy soils is often poor because of low moisture and nutrient levels (74). Moisture conditions are favorable if the ground water table occurs between 18 inches and 5 feet below the soil surface. A water table shallower than 18 inches may interfere with aeration and thus be detrimental (86). Heavy clay soils also do not promote the best growth because of poor aeration (74).

The major limiting factor in the central Rocky Mountains is rockiness of the soil which, by hindering the lateral spread of the shallow roots and interfering with their tendency to rise close to the surface,

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4/ Correspondence with Edward M. Gaines, Rocky Mountain Forest and Range Experiment Station, June 26, 1956, on file at Lake States Forest Experiment Station.

5/ Correspondence with Fred G. Wilson, Box 108, Madison, Wis., June 1956, on file at Lake States Forest Experiment Station.

restricts the reproductive ability of the tree and its general development (8). In this area and also in the Southwest, the species develops best on flats and gentle slopes and in small valleys with rich, deep soil and plenty of moisture. Smaller trees are found on the thin rocky soils of high mountain slopes and ridges (79). In eastern Oregon and Washington the presence of aspen is usually associated with a subirrigated soil.[6]

Physiographic Factors

Near its northern limit quaking aspen is found at elevations up to 5,800 feet (79). To the south in its western range the species ascends to higher altitudes although it still occurs at sea level as far south as the State of Washington. In Lower California, however, near the southern limits of its range, it does not occur below about 8,000 feet (85). In Arizona and New Mexico the species is most abundant between 6,500 and 10,000 feet where it occurs mainly on cool, shaded mountain slopes, in canyons, and along streams (43). These are also the approximate altitudinal limits for aspen of commercial size in Colorado and Utah, although the tree is generally small and of poor form below about 7,000 feet.[7] At either of its altitudinal limits the tree is poorly developed. In very high exposed places it becomes stunted with the stem bent or almost prostrate (79), whereas at its lower limit it is a scrubby tree growing along creeks (8).

In Maine aspen occurs to within 20 feet of tidewater, although growth is better at higher elevations (85). Elevation, however, is generally of much less consequence in affecting the distribution of aspen in the eastern part of its range than in the western part.

In Alaska and western Canada the species is most abundant on south and southwest aspects (45, 78). It is not uncommon on such aspects in the western mountains of the United States. Development is rather poor on these sites, however, because of their excessive droughtiness (8, 45). In the prairie provinces of Canada, particularly near the border between prairie and woodland, grass occupies these dry south and west slopes of the rolling terrain, and quaking aspen is confined to the cooler and moister north and east slopes, and to the depressions (48). The best stands of aspen in the Southwest also occur more frequently on the northerly slopes where more favorable moisture conditions prevail.[8]

6/ Correspondence with Leo Isaac, Pacific Northwest Forest and Range Experiment Station, July 2, 1956, on file at Lake States Forest Experiment Station.

7/ Correspondence with Lake S. Gill, Rocky Mountain Forest and Range Experiment Station, July 9, 1956, on file at Lake States Forest Experiment Station.

8/ See footnote 4 on page 4.

Biotic Factors

Quaking aspen grows in conjunction with a large number of trees (table 1) and shrubs over its extensive range.

Shrub species commonly associated with quaking aspen in the eastern portion of its range include beaked hazel (*Corylus cornuta*), American hazel (*C. americana*), mountain maple (*Acer spicatum*), speckled alder (*Alnus rugosa*), green alder (*A. crispa*), raspberry (*Rubus idaeus*), and various species of *Ribes* and *Salix*. Additional species occurring with quaking aspen in the prairie provinces include snowberry (*Symphoricarpos* spp.), mooseberry (*Viburnum pauciflorum*), limber honeysuckle (*Lonicera dioica*), redosier dogwood (*Cornus stolonifera*), Saskatoon serviceberry (*Amelanchier alnifolia*), common chokecherry (*Prunus virginiana*), Bebb willow (*Salix bebbiana*), and several species of *Rosa*. The latter two also occur in Alaska plus such additional species as Scouler willow (*Salix scouleriana*), littletree willow (*S. arbusculoides*), bearberry (*Arcostaphylos uva-ursi*), russet buffaloberry (*Shepherdia canadensis*), and mountain cranberry (*Vaccinium vitis-idaea*). In the Rocky Mountains, shrubs commonly occurring with aspen include mountain snowberry (*Symphoricarpos oreophilus*), creeping mahonia (*Mahonia repens*), Fendler woods rose (*Rosa woodsi fendleri*), myrtle pachistima (*Pachistima myrsinites*), and scarlet elder (*Sambucus pubens*).

Bracken fern (*Pteridium latiusculum*) frequently grows in conjunction with quaking aspen in the eastern portions of its range. Some investigators feel that a correlation exists between the height of the bracken and aspen site quality, with the best aspen occurring where the bracken is tallest (74).

LIFE HISTORY

Within its natural range quaking aspen follows a distinct pattern of reproduction, growth, and development, influenced both by hereditary characters and environmental factors. Much of aspen's life history is bound up with fire. Quaking aspen is essentially a short-lived, rather fast growing pioneer species distributed over a wide geographic range and growing on a great variety of soil and site conditions.

Table 1.--Common tree associates of quaking aspen in various parts of its range

Species	Eastern U.S. and Canada[1/]	Western U.S. and Canada[2/]	Near prairie border[3/]	Alaska[4/]
Balsam poplar (*Populus balsamifera*)	x	x	x	x
Bigtooth aspen (*P. grandidentata*)	x			
Paper birch (*Betula papyrifera*)	x	x	x	x[5/]
Yellow birch (*B. alleghaniensis*)	x			
Balsam fir (*Abies balsamea*)	x			
White spruce (*Picea glauca*)	x	x	x	x
Black spruce (*P. mariana*)	x	x		
Eastern white pine (*Pinus strobus*)	x			
Red pine (*P. resinosa*)	x			
Jack pine (*P. banksiana*)	x			
Sugar maple (*Acer saccharum*)	x			
Red maple (*A. rubrum*)	x			
Northern red oak (*Quercus rubra*)	x			
Northern pin oak (*Q. ellipsoidalis*)	x			
Bur oak (*Q. macrocarpa*)	x		x	
Pin cherry (*Prunus pensylvanica*)	x		x	
American elm (*Ulmus americana*)	x		x	
Basswood (*Tilia americana*)	x			
Black ash (*Fraxinus nigra*)	x			
Green ash (*F. pennsylvanica*)	x		x	
Tamarack (*Larix laricina*)	x	x		
Northern white-cedar (*Thuja occidentalis*)	x			
Alder (*Alnus* spp.)		x		
Box elder (*Acer negundo*)			x	
Lodgepole pine (*Pinus contorta*)		x		
Ponderosa pine (*P. ponderosa*)		x		
Douglas-fir (*Pseudotsuga menziesii*)		x		
Subalpine fir (*Abies lasiocarpa*)		x		
White fir (*A. concolor*)		x		
Engelmann spruce (*Picea engelmannii*)		x		
Sitka spruce (*Picea sitchensis*)		x		
Blue spruce (*P. pungens*)		x		
Black cottonwood (*Populus trichocarpa*)		x		

1/ After Kittredge and Gevorkiantz (39), and Society of American Foresters (72).

2/ After Society of American Foresters (72), Cottam (17), and Sudworth (78).

3/ After Society of American Foresters (72), and Moss (48).

4/ After Lutz (45).

5/ Varieties *humilis* and *kenaica*.

Seeding Habits

Flowering and Fruiting

The flowers of quaking aspen are borne in catkins or aments. Most reference works consider the flowers to be typically imperfect (unisexual) and the trees dioecious, i.e., with the sexes segregated such that individual trees are wholly female or male. Results of recent studies in Massachusetts and Minnesota, however, indicate that wild seedling-origin populations of the species may contain relatively high percentages of trees bearing perfect (bisexual) flowers, or imperfect flowers of both sexes. The bearing of perfect flowers is by far most common and appeared in 10 to 20 percent of the predominantly female trees and only 4 to 5 percent of the predominantly male trees (56, 65).

Trees of the two sexes are unevenly distributed, there often being many male trees to one female tree (6, 78). Recent studies in the eastern United States indicate a ratio of males to females of about 3 to 1 in wild populations (52, 56). Most of the trees in a given locality, of course, may be either all male or all female if they are of sucker origin and comprise a clonal island, i.e., if all have arisen from the roots of a single parent tree.

Some empirical observations further suggest the possibility that a positive correlation may exist between maleness and such desirable characteristics as vigor, disease resistance, and good stem form (53).

Aspen flowers generally appear in April or May before the leaves develop. Pollination is accomplished by wind, and the fruits usually ripen in May or June, about 4 to 6 weeks after flowering. The fruit is a one-celled capsule containing many small brown seeds each of which is surrounded by tufts of long, white, silky hairs (82). There are from 2½ to 3 million of the tiny seeds per pound (39).

Seed Production and Dissemination

Good seed crops are produced every 4 or 5 years with light crops in most intervening years (82). Although great quantities of seed may be produced in a given year, many of the female trees in any given locality may not bear seed that year (39). The minimum commercial seed-bearing age is 20 years, and the optimum seed-bearing age about 50 to 70 years (82).

The viability of fresh fertile seeds is high, but normally of short duration. Under favorable natural conditions viability lasts only 2 or 3 weeks after maturity (39), and may be much less under unfavorable conditions. However, seed has maintained reasonable viability for 8 weeks when stored in an open dish out of direct sunlight at 71° F. and a 40- to 50-percent relative humidity (82). In another study seed dried for 3 days and then stored in sealed containers at 41° germinated 97 percent at the end of 1 year (82).

Seed dispersal takes place within a few days after ripening. The seeds, buoyed by the long silky hairs, can be carried for miles by air currents (78). Water also serves as an agent of dispersal.

General reports have been that quaking aspen seldom produces seed in the West and that the seed which is produced often is not viable (6, 42). However, at least one collector (54) has been successful in obtaining aspen seed from each of the western states in which the species occurs. He feels that inaccessibility of many of the higher altitude stands at the time of flowering has helped to perpetuate the belief that western aspen is fruitless. Other investigators have also encountered young aspens in the West of unquestionable seedling origin (22, 41).

Vegetative Reproduction

Aspen reproduces vigorously by means of root suckers (fig. 2 on next page), much less commonly by root collar sprouts, and occasionally from stump sprouts (6).

The root suckers are produced from sucker buds on the shallow lateral roots, usually from those which are within 3 or 4 inches of the soil surface (20, 64). Although dormant sucker buds formed in previous years may be present and locally numerous on a root, laboratory tests showed that 95 percent of 174 successful suckers originated from buds formed in the same season (64). In greenhouse tests suckers originating from new buds grew more vigorously than those arising from dormant buds stimulated to renewed growth.

A few suckers will arise almost every year, even in uncut stands, but for abundant and vigorous sucker reproduction strong light and heat must reach the forest floor (90). Laboratory experiments indicate that temperature may be more important than light in bringing about the initial formation of suckers; with soil temperatures held constant, suckering was abundant both in reduced light and in full light (64). However, strong light is necessary for the continued vigorous development of the young suckers. Experiments showed that increased light intensity stimulated the development of new roots, and resulted in a more even rate of height growth and better secondary growth of sucker stems than occurred under reduced light intensities (64).

Figure 2.--Two aspen suckers that have developed from a 23-year-old parent root.

Suckers are initially sustained by the root system of the parent tree, but they form their own root systems with amazing speed. A marked thickening of the parent root usually takes place at the point of sucker origin, but only on the side away from the parent tree, indicating that translocation of food material produced in the sucker is toward the growing tip of the root (20).

Suckers can arise from the roots of badly decayed trees as well as from the roots of healthy trees (85). A study in Minnesota revealed no evidence that suckers are infected by the parent stump through the roots, and it was noted that heartrot seldom extends very far into the roots, usually terminating in the base of the stump (67).

In general the number of suckers produced is proportional to the degree of cutting, with the greatest number arising after a complete clear cut, and progressively fewer arising as more of a residual stand is left. In Minnesota, a study involving late fall cutting of a 43-year-old stand to various diameter limits showed suckers arising as follows: cut to 10-inch diameter limit--1,980 suckers per acre; 9-inch limit--2,115 suckers; 8-inch limit--4,500 suckers; clear-cut--6,830 suckers (90).

Various other factors also influence the number of suckers produced. Light burning on heavily cut areas increases the number of suckers which develop and also stimulates their growth during the first year after burning, due apparently to the increased heat absorption of the blackened surface (69). Repeated burning actually tends to thicken a stand because it stimulates sucker development and also prepares the soil for seedling establishment (70).

Disking has proved effective in stimulating suckering on understocked aspen areas (91) and on areas where cull aspen trees have been left standing (90). Rows of suckers often appear along furrows plowed to prepare such areas for the planting of conifers.

Poisoning of defective residuals with ammonium sulphamate has also been used successfully to increase suckering without any apparent adverse effects on sucker growth or vigor (83).

The time of year at which cutting is done exerts some influence on the number of suckers which arise as well as on their vigor and survival (6, 76). Late fall, winter, or early spring cutting, i.e., dormant season cutting, generally produces a vigorous sucker crop during the next growing season. Summer cutting, on the other hand, often produces a poorer stand, due partly to competition from brush and other vegetation and perhaps also to the depletion of stored food in the roots during the active growing season (89). However, some studies show that within 2 years after logging the number of suckers present on cutover areas is practically the same for both winter-cut and summer-cut stands (64).

The number of suckers produced following cutting is related to the age of the parent stand; more suckers are produced from the older parent trees provided they are vigorous at the time of cutting (39, 76).

Although the roots of quaking aspen have tremendous regenerative capacity, they cannot withstand unlimited abuse. If all new suckers are destroyed by cutting or heavy grazing, such as by sheep, for three successive years, food materials in the roots become exhausted with no opportunity for replenishment and suckering usually ceases (6, 63).

Normally the species roots very poorly from stem cuttings. However, by using cuttings from 1-year-old sprouts and treating them with indolebutyric acid, Snow (71) succeeded in rooting about 65 percent of them. Propagation by root cuttings is quite easy. Good success has also been attained by grafting quaking aspen scions onto short unrooted stem cuttings of balsam poplar or willows. The latter root readily and later the aspen scions also root and continue to grow on their own roots.[9/] Quaking aspen scions can also be grafted successfully onto bigtooth aspen seedlings.[9/]

9/ Unpublished information supplied by Scott Pauley, School of Forestry, University of Minnesota, 1956.

Seedling Development

Establishment

Ripe aspen seeds are not dormant and natural germination takes place within a day or two after dispersal if a suitably moist seedbed is reached (82). Germination takes place unhampered even when the seeds are totally submerged in water; also, it does not depend on light and will take place at any temperature between 32° and 95° F. if there is sufficient moisture (23).

The primary root of the tiny seedling makes very slow growth for several days, and during this critical period the young plant depends upon a brush of long delicate hairs to perform the absorptive functions (49). These hairs arise from the junction of the root and the hypocotyl and, although they provide a large absorbing area, they are effective only if the surface soil is moist.

Even after passing this first critical period, the seedlings are still highly susceptible to damage from heat, drought, and fungi. Also, during the first year, freedom from competing vegetation is essential (70). Seedlings may attain a height of 12 inches or more during this first year and develop an 8- to 10-inch taproot (70). During the second and third years widespreading lateral roots are developed.

Reproduction of quaking aspen from seed is comparatively unimportant in regenerating existing stands, although this method has been important in establishing the species on a vast area of cutover and burned-over land that was formerly in other forest types (39).

Early Growth

Although seedling height growth is usually not equal to that of suckers, it exceeds the height growth of all of the species' common associates except pin cherry (20).

Growth of the young trees is particularly rapid during about the first 20 years, and slows down somewhat thereafter (85, 89). High mortality, however, characterizes young aspen stands regardless of origin. In both seedling and sucker stands natural thinning is rapid, and trees that fall below the general crown level stop growing and die within a year or two (70). A Wisconsin survey of cutover aspen areas revealed that only about one-eighth as many stems were present 9 years after cutting as were present 2 years after cutting (76).

Observations on various growth phenomena have been made for quaking aspen in the Upper Peninsula of Michigan for periods up to 10 years (table 2). The average period of height growth there is about 80 days whereas that of circumference growth is about 105 days. In the vicinity of Cedar Lake, Ontario, the circumference growth period is about the same length as in Upper Michigan but runs about 11 or 12 days later (10).

Table 2.--Phenological data for quaking aspen in Upper Michigan 1/

Growth phenomenon	Average date	Number of years observed 2/
Leaf buds swelling	May 6	5
Beginning to leaf out	May 15	10
Full leaf	June 5	10
First flowering	May 2	4
Full bloom	May 11	5
Fruit matured	May 28	6
Seed falling	June 3	5
Start of leaf coloring	Sept. 19	6
Maximum leaf coloring	Oct. 4	8
Start of leaf fall	Oct. 2	8
Leaf fall completed	Oct. 17	7
Start of height growth	May 23	6
End of height growth	Aug. 10	4
Start of circumference growth	May 19	6
End of circumference growth	Aug. 31	6

1/ Unpublished data, Lake States Forest Experiment Station.
2/ Observations were made in the years 1927 to 1936.

On the lower slopes of the San Francisco Mountains in northern Arizona, elevation 8,900 feet, growth phenomena occur as follows (57): Vegetative buds swelling, May 10-30; vegetative buds elongating or opening, May 20-June 10; leaves coming out, June 5-15; leaves falling, October 10-30; period of active growth, May 20-September 10.

A study of the seasonal moisture variations of quaking aspen in Minnesota revealed that the period of highest moisture content of the wood occurs during the fall and winter rather than during the spring and summer (34).

Numerous factors other than competition cause injury or mortality in young stands. Very young trees are sometimes killed by bark-eating mammals such as the meadow mouse (*Microtus pennsylvanicus*) and the snowshoe hare (*Lepus americanus*) which may girdle the stems at or near the ground line (48, 75). Also, larger animals such as the mule deer (*Odocoileus hemionus*), the white-tailed deer (*O. virginianus*), and the moose (*Alces alces*) will frequently do serious damage to aspen reproduction by their browsing (40, 51, 75), and by rubbing their antlers against the young stems. Elk (*Cervus canadensis*) also cause considerable damage of this latter type (51).

In Ontario, a canker caused by *Neofabraea populi* has been noted on some of the younger aspen, usually on trees 3 to 6 years old and not over 1½ inches in diameter (81). Not many of the afflicted trees are killed, however.

Shoot blight of aspen caused by *Napicladium tremulae* is periodically severe. The young shoots bend double, darken in color, and dry out (14).

Two cytospora cankers (*Valsa sordida* and *V. nivea*) occur throughout the range of quaking aspen. They are generally of a secondary nature and attack trees, both young and old, already weakened by other causes (14, 68).

Figure 3.--Well-stocked aspen stand in northern Minnesota.

In the West *Sclerotinia bifrons* causes a leaf spot on trees of all ages. When the disease is severe small trees may be killed, but those that are 8 feet or taller rarely die (59). *Marssonina populi* causes a leaf spot and shoot blight on aspen that is especially prevalent and damaging in the western states. It is responsible for occasional severe defoliation, and severe, repeated infection can cause mortality (47).

Larvae of the poplar borer (*Saperda calcarata*) often kill small trees by girdling beneath the bark (18). Black carpenter ants (*Camponotus herculeanus pennsylvanicus*) frequently make use of the tunnels provided by this borer, thus causing further damage in young stands (89). Also, the poplar-gall saperda (*Saperda concolor*) may cause considerable damage to the branches of small trees.

Sapling Stage to Maturity

Growth, Longevity, and Yield

Over much of its range, quaking aspen is a small to medium-sized, fast-growing, and generally short-lived tree (see cover picture). Under the best of conditions, however, it may attain a height of 100 feet and a diameter of about 3 feet (30, 66). In southern Utah a tree was found measuring 76 feet in height and 9 feet 10 inches in circumference (37.6 inches in diameter) at breast height (1). Aspen attains a maximum age of about 200 years in the Rocky Mountain region, although only a few trees retain their vigor until this age (79).

The largest sizes are generally attained in a belt bordering the mid-continental prairie region (66), although the species also attains heights of about 100 feet in certain parts of the Lake States (89) and on the slopes of the San Francisco Mountains in northern Arizona (66).

Although growth is slower in the West than in the East, decay also progresses more slowly (8), and hence rotations can be longer. For quaking aspen in Utah a pathological rotation of 80 to 90 years has been suggested (46). On the best sites in the Lake States, such as occur in portions of Minnesota, the pathological rotation is about 55 to 60 years; in much of Wisconsin and Michigan the rotation must be even shorter.

The rotation, yield, and development of aspen in well-stocked, unmanaged stands in northern Minnesota (fig. 3) can be summarized as follows (89):

1. Good sites.--Aspen reaches sawlog size at the rotation age of about 55 years. Gross yields of 9,100 board-feet or 46 cords per acre and higher are attainable.

2. Medium sites.--Small sawlogs and pulpwood can be produced at the rotation age of about 45 years. Gross yields of 5,000 board-feet or 32 cords per acre are attainable.

3. Poor sites.--Much of this aspen is noncommercial under present conditions. At a rotation age of about 30 years it seldom reaches more than pulpwood size, and gross volume per acre may be only 5 cords.

The relationship between total height and age varies by sites (table 3) in the Lake States (89).

Table 3.--Total height of aspen at various ages, on various sites (26)

Age (years)	Total height[1/] in feet on the following sites:				
	Excellent	Good	Medium	Poor	"Off-site"
20	44	39	34	28	23
30	59	51	44	37	29
40	70	62	53	44	35
50	79	69	60	50	39
60	87	76	66	55	--
70	93	82	70	59	--
80	98	86	74	--	--

1/ Average for dominant trees in well-stocked even-aged stands.

That excellent growth is also attainable in the Southwest is evidenced by one study in which a residual stand of aspen 2 to 8 inches in diameter grew an average of 1.42 cords per acre per year over a 10-year period (84). This was on a good aspen site that had been commercially cut to a 9-inch diameter limit, leaving a residual stand of 857 smaller trees per acre.

Reaction to Competition

In both the eastern and western parts of its range quaking aspen is rated as very intolerant (9), a characteristic which it retains throughout its life (78). Because of its intolerance of even side shade the species shows excellent natural pruning and produces long clean stems when such side shade is present (78).

The species is characterized by a pronounced ability to express dominance (70), and overstocking to an extent sufficient to cause stagnation of growth is extremely rare (39). Nevertheless, the growth rate can be decidedly increased by artificial thinning, and response is best if the thinning is done at an early age (11, 89). The species is thin-barked, however, and a heavy thinning may result in considerable injury from exposure and sunscald (11).

Place in Succession

Quaking aspen is an aggressive pioneer species. It has tremendous capacity to colonize burns, and it can spread and hold the land it has invaded even though subjected to fires at intervals as short as 3 years (70). Following fire, the rapid first-year growth of the suckers that spring up generally enables the species to take and maintain a dominant position with regard to other vegetation throughout its 40 to 70 years of vigorous development (38).

While it reproduces most abundantly on areas that have been heavily cut and then burned, quaking aspen will also invade pine stands and other types following a fire that only thins the stand (70). However, brush species often thrive better than aspen reproduction under partial shade and may offer the young aspen serious competition in stands where a portion of the ov :story is left (88).

In portions of the northeastern United States quaking aspen occurs as an old-field type. The species can even invade grassland areas such as occur in northern and central British Columbia (15), and in the prairie provinces of central Canada (48) if fire is kept out.

Because the species does not reproduce well under even very light shade, it is regarded over most of its range as a temporary forest type that will eventually be replaced by its more shade-enduring associates if natural succession is allowed to take place (62, 70, 78).

An estimate of the rate of this conversion in Minnesota, Wisconsin, and Upper Michigan (33) shows the following trend, based on Forest Survey plot data: (1) By the year 1990 nearly one-third of the aspen-birch type may be completely converted to other types, mainly northern hardwoods, spruce-fir, and low-value types such as scrub oak, red maple, and ash-elm; (2) an additional 14.5 percent is undergoing partial conversion; (3) the remaining 53.1 percent shows no definite conversion trend at present.

Of course, a reverse trend is also taking place constantly where other forest types are being cut, burned, or otherwise disturbed and are subsequently replaced by aspen.

In the central Rocky Mountains, outside of the distribution of lodgepole pine, aspen constitutes the typical fire sub-climax at the lower elevations in the subalpine forest zone (73). This also holds true for the species in the Southwest.[10/] The rate of ultimate restocking by spruce and fir depends largely on the presence of seed trees.

In certain areas some investigators feel that quaking aspen should be considered as a permanent type. Fetherolf (24) regards the species as permanent in the semi-arid intermountain region of Utah, Nevada, and southern Idaho, and contends that within a certain altitudinal zone there is no native conifer that can replace it either with or without the help of fire. However, Baker (5) attributes this apparent permanency to the complete destruction of all seed trees of those species such as Douglas-fir that could regain possession of the area if a source of seed were available.

Elsewhere, quaking aspen has also been regarded as a permanent type. In Alaska, E. G. Stoeckeler[11/] regards it as a climax type on excessively dry slopes having a southerly or westerly exposure. Also, the species is considered to be climax in portions of Manitoba and Saskatchewan (13), as well as in southern Alberta near the prairie border (48) and in the Steens Mountains of Oregon.[12/]

Limiting Factors

Some of the destructive agencies that kill or injure very young aspen trees have already been mentioned, including a few that are important in the older stands as well.

10/ See footnote 4, page 4.

11/ Stoeckeler, E. G. Identification and evaluation of Alaska vegetation from airphotos with reference to soil moisture and permafrost conditions. U. S. Corps of Engineers, St. Paul Dist., Field Oper. Branch, Permafrost Div. 103 pp. 1948. (A preliminary paper; processed.)

12/ See footnote 6, page 5.

By and large, the enemies of greatest economic significance are the wood-rotting fungi and the cankers. The foremost of the first group is the false tinder fungus (Fomes igniarius), which is present on the species throughout its range (46). It causes a typical white rot of the heartwood, but it also attacks the sapwood and in the final stage it may cause decay throughout the entire stem (89). Of lesser importance, but also common, is red heart caused by Radulum casearium.

Several butt-rotting fungi, including Fomes applanatus, Armillaria mellea, and Pholiota spp., attack aspen. In the Rocky Mountains Fomes applanatus, because of the windfall it induces, may be nearly equal in destructiveness to F. igniarius.[13]

Some early investigators felt that site quality had little or no influence on the prevalence of decay (67), but later studies indicate that the amount of decay is affected by site and also by individual tree vigor, the greatest decay being associated with poor sites and low vigor trees (4, 39, 89).

Hypoxylon canker (Hypoxylon pruinatum) is one of the most serious diseases of quaking aspen, particularly in the eastern portions of its range. It causes heavy losses, especially in the younger stands (14, 89). In Wisconsin 24 percent of all aspen was found to be infected (28). The canker may kill trees directly by girdling, or may so weaken them at the point of infection that breakage ultimately occurs (14). The incidence of the canker is not correlated with site index or tree vigor (2, 12), although the damage is greater on poor sites because the slower growing trees are exposed to infection longer before reaching merchantable size. The canker is generally more common in stands of low density than in well-stocked stands (2). Recent studies seem to indicate that most cankers originate in the immediate vicinity of a dead branch stub or an old scar (3).

In Michigan some correlation appears to exist between insect attacks on quaking aspen and the development of the canker (27).

In the Rocky Mountain region Hypoxylon canker is a relatively unimportant cause of loss. Here the black canker or sooty-bark canker caused by Cenangium singulare is a much more serious disease (19).

Bacterial wetwood is rather common in aspen, and occasionally Nectria canker, caused by Nectria parasitica, is found on the species.

Among the insects that cause serious damage to aspen, the two most important are the poplar borer (already mentioned) and the forest tent caterpillar (Malacosoma disstria). The poplar borer is a primary

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13/ See footnote 7, page 5.

insect, but unlike some of aspen's other serious enemies it appears to be more common on poor sites than on good sites, at least in Minnesota (16). Some entomologists, however, feel that its abundance is correlated with stand density rather than site, and point out that attack by the poplar borer can be encouraged by over-thinning a stand.[14/]

The forest tent caterpillar may cause serious reduction in diameter growth of aspen, particularly if defoliation occurs for several successive years (25). In the Upper Peninsula of Michigan some areas have been defoliated for three or more successive years, resulting in a high rate of mortality and the ruining of some stands for commercial purposes.[15/]

In the East, quaking aspen is a favored host for the gypsy moth (*Porthetria dispar*) and the satin moth (*Stilpnotia salicis*). The large aspen tortrix (*Archips conflictana*) attacks quaking aspen from New York to Utah and north to Alaska and Labrador, periodically causing noticeable defoliation (18).

Certain wildlife species may seriously damage aspen stands. Beaver (*Castor canadensis*) feed on the young tender bark and shoots, and often cut down large numbers of trees near their colonies (51). In the West, the red-naped sapsucker (*Sphyrapicus varius nuchalis*) and Natalie's sapsucker (*S. thyroideus natalie*) may seriously scar numerous trees (51). Similar damage is caused in the East by the yellow-bellied sapsucker (*S. varius varius*).

Locally, a high population of porcupines (*Erethizon dorsatum*) can do considerable damage to aspen crowns, not only directly but also indirectly by making the crowns more susceptible to attack by insects and diseases.

Relatively minor damage is caused by such woodland birds as the ruffed grouse (*Bonasa umbellus*) and the sharp-tailed grouse (*Pedioecetes phasianellus*), which feed on the buds of quaking aspen; ruffed grouse also feed on the leaves during the summer months (16).

Aspen is fairly susceptible to fire damage. Fires may kill trees outright, cause basal scars which eventually serve as avenues of entrance for wood-rotting fungi, or, if repeated, reduce height growth as much as 6 to 25 feet in 50 years according to one study (74).

14/ Correspondence with Samuel A. Graham, School of Natural Resources, University of Michigan, July 1956, on file at Lake States Forest Experiment Station.

15/ Correspondence with Maurice W. Day, Superintendent of Dunbar Forest Experiment Station, Michigan State University, June 27, 1956, on file at Lake States Forest Experiment Station.

Severe winds may damage aspen crowns, thereby reducing growth and increasing the chances of decay.

SPECIAL FEATURES

The wood of aspen is nearly white and has a fine, uniform texture; it is practically odorless and tasteless (87). Its chief uses have been for pulpwood, boxes and crating, excelsior, and matches (42), although it has also been used for core stock, interior trim, furniture, venetian blinds, cabin logs, construction lumber, railroad ties, fence posts, and toys and novelties (87).

The bark of quaking aspen contains an astringent, which early American pioneers extracted and used as a substitute for quinine (30).

Chemicals that have been used to kill quaking aspen with varying degrees of success include ammonium sulphamate, 2,4-D esters, 2,4,5-T esters, combinations of "D" and "T" esters, and DNOSP (dinitro ortho secondary butyl phenol). The last 3 have all achieved complete top kill of young trees by 1 application; the first 2 have achieved complete top kill by repeated application (61). Type of application and best season for attaining success vary with the different chemicals.

RACES, HYBRIDS, AND OTHER GENETIC FEATURES

Little scientific information is available as to the development of climatic races, although there is one variety (*Populus tremuloides* var. *aurea*) confined to the West, and another variety (*P. tremuloides* var. *vancouveriana*) confined to the vicinity of Vancouver Island and Puget Sound. Both of these varieties are probably climatic races (82).

A dwarf variety of the species occurs in southern Ontario and has been used to some extent in grafting experiments in Canada (32).

Throughout the mountains of Utah and in neighboring States there are distinct colonies of the species (variety *aurea*) that attain full leaf 2 or 3 weeks earlier than the major stand surrounding them (7, 17). A segment of this prevernal leafing form appears to be a response to temperature controls, but in general the early-leafing colonies probably represent distinct genetic strains (17).

Natural hybrids of P. tremuloides x P. grandidentata are not uncommon in central and eastern Massachusetts (55) and have also been reported in Canada. Doubtless these natural hybrids occur to some extent throughout the common range of the two species (55). Such hybrids are fertile, and consequently back-crosses with the parent species are also possible.

Natural hybrids between the European P. alba and P. tremuloides occur in a number of localities in the vicinity of Ottawa (58). This cross produces good viable seed, as does a cross of P. canescens x tremuloides (31).

Quaking aspen can also be crossed readily with its close European relative P. tremula, and early observations on some field plantings show this hybrid to be a fast grower with good survival (77). In Sweden and Denmark this hybrid has been mass produced since shortly after World War II, and is in strong demand because of its vigorous growth characteristics and its resistance to certain diseases.

Numerous other artificial crosses under observation for possible commercial use are reported by Heimburger[16/] [17/] and include the following:

Populus tremuloides x adenopoda
P. tremuloides x davidiana
P. tremuloides x (alba x tremuloides)
P. tremula x (alba x tremuloides)
P. (grandidentata x tremuloides) x grandidentata

According to present information, the vegetative cells of ordinary wild aspens, as well as those of nearly all aspen hybrids, are each internally regulated by exactly 38 chromosomes in two similar sets of 19 each (35).

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Ensuing reports by the Station will cover the following species:

Bigtooth aspen	Jack pine
Basswood	Balsam poplar
American elm	White spruce
Slippery elm	Tamarack
Black maple	Northern white-cedar
Sugar maple	

SOME RECENT STATION PAPERS

Forest Management Lessons from a 1949 Windstorm in Northern Wisconsin and Upper Michigan.
J. H. Stoeckeler and Carl Arbogast, Jr.
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The Timber Resource of North Dakota.
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